

SOUND CONDUCTION IN THE FOSSIL ANOMODONT
LYSTROSAURUS

By

T. H. BARRY

South African Museum, Cape Town

(With 1 plate and 3 text-figures)

CONTENTS

	PAGE
Introduction	275
Description	275
Discussion	277
Summary	280
Acknowledgements	281
References	281

INTRODUCTION

In a paper published in 1963, the author drew attention to the marked degree of variation that exists in the structure of the sound-conducting apparatus of many closely related genera of living reptiles and expressed the view that the structure of the middle ear region in many fossil forms supplied circumstantial evidence to substantiate the view that a marked degree of variation could also have existed in fossil mammal-like reptiles, not only between sub-orders but also within some of them. The evidence presented in this paper would seem to lend support to this view.

DESCRIPTION

In 1964 Mr. Chris Gow of the South African Museum drew my attention to a thin rod-like bone attached to the ventro-lateral surface of the right stapes of a specimen of *Lystrosaurus murrayi* (Huxley) which he had prepared with acid (fig. 1, plate XV, B). From its base the rod extends antero-medially at an angle of approximately 45° to the long axis of the stapes, following a course roughly parallel to the quadrate ramus of the pterygoid. In lateral view it can be seen that the rod curves downward and then upward to end free (plate XV, A). On the left side both the stapes and the rod are absent.

As a stapedia process of this nature has not been reported for any Anomodont it was essential to ascertain whether this attachment represented a chance fusion during life or afterwards, or whether this association actually existed during life.

By careful removal of the matrix surrounding the base of the rod it was found that the rod could be lifted off the stapes. The area of attachment on the stapes proved to be smooth, indicating that the attachment of the rod to this area of the stapes represents a postmortem association. However, further examination revealed the existence of a triangular, flattened, slightly rugose area on the ventro-medial surface of the stapes not previously recorded for *Anomodonts*. As will be shown later this depression probably represents the original area of attachment of the rod to the stapes.

This discovery led to the preparation of a second skull, that of *Lystrosaurus natalensis* (specimen No. K.1165 of the South African Museum collection). In this specimen both stapes are present, but they are displaced anteriorly to lie between the lower jaw rami. A long, curved, rod-shaped process, slightly expanded distally, extends from the ventro-lateral border of the left stapes (plate XV, D). The right stapes is without this rod-like process but a slender bone, conforming to its general configuration, lies slightly in front of it. A roughly triangular, flattened area on the ventro-medial surface of the right stapes shows where this rod had probably been attached.

Removal of the matrix covering the area of contact between the rod and the stapes on the left side revealed that the two bones were not actually fused but had become cemented together by the matrix. Of interest, however, is that the area of contact partly overlaps an indented area similar to that found on the right stapes. The anterior ends of both rods are unfinished and slightly expanded indicating that the bones were probably continued in cartilage.

Conditions very similar to these were found in two specimens of *Lystrosaurus verticalis*. In the first the right stapes only was still in position, the left stapes and two rods lying grouped together a short distance forward. Both stapes show the triangular flattened area found in *L. natalensis*. After cleaning it was found that the proximal part of each rod followed the outline of and could be perfectly fitted on to the triangular area of the corresponding stapes. In this position the distal ends of the rods do not meet in the midline.

The second specimen of *L. verticalis* had both stapes in position but no rods were found. However, the triangular areas on the stapes are well developed and very similar to those found in the specimen previously mentioned.

In another fossil specimen investigated, the type of *Lystrosaurus oviceps* (specimen No. 641 of the South African Museum collection) both stapes are present and in position. Two curved rods, outwardly similar to those described for the other *Lystrosaurus* specimens, lie in front of but at a deeper dorsal level than the two stapes (plate XV, C). Unfortunately part of the ventral surface of the skull, including the ventral surface of the stapes, had been scoured away, obliterating any evidence of a possible attachment to the stapes.

In *Lystrosaurus declivis* in which the stapes is well preserved, there is no indication of the ventro-medial flattened areas found in *L. murrayi*, *L. natalensis* and *L. verticalis*. This suggests that there was a variable relationship between the rod-like process and the stapes within the genus. In *L. murrayi*, *L. natalensis*

and *L. verticalis* the connection was probably synovial, in *L. declivis* it could have been weakly synchondrotic, but without leaving a mark on the stapes, or it could have been syndesmotic or free.



FIG. 1. *Lystrosaurus murrayi*, reconstruction of ventral view of the middle ear region with ceratohyals in position.
C.H., ceratohyal; S.T., stapes.

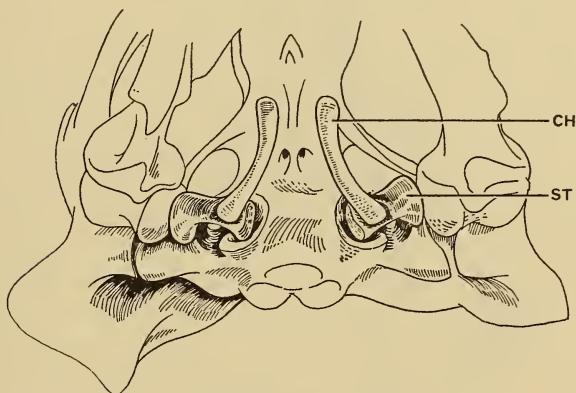


FIG. 2. *Lystrosaurus verticalis*, reconstruction of ventral view of the middle ear region with ceratohyals in position.
C.H., ceratohyal; S.T., stapes.

DISCUSSION

Reconstruction of the missing stapelial attachment of the first specimen, *L. murrayi*, shows that, as in the case of *L. verticalis*, the rods occupy a position normally associated in recent reptiles with the ceratohyals or ceratobranchials I or II of the hyobranchial skeleton. The fact that the distal ends of the rods do not meet in the mid-line would seem to strengthen this view as this area is normally occupied by the median basihyal. The absence of any evidence of the latter would seem to indicate that it was cartilaginous.

Conditions in living reptiles and mammals favour the assumption that the rods represent fossilized ceratohyals, for in both living groups an embryonic connexion exists between the ceratohyal and parts of the sound-conducting apparatus; in reptiles with the extra-columella and in mammals with the stapes.

In *Lacerta* and many other lacertilians the ventrally projecting pars accessorius posterior (processus interhyalis) represents the stump of the ligament which connected the ceratohyal with the extra-columella in earlier developmental stages. This is also the case in early developmental stages of the chelonians *Chrysemys* (Smith, 1914) and *Testudo* (Bender, 1911). In the adult stages the ceratohyal can be free or it can become attached to the skull.

In *Sphenodon* and *Crocodylus*, however, a direct connexion is retained throughout life between the ceratohyal and the columella. In the adult the connexion is cartilaginous, resulting, in *Sphenodon*, in the entire hyobranchial skeleton being suspended from the columella (fig. 3).

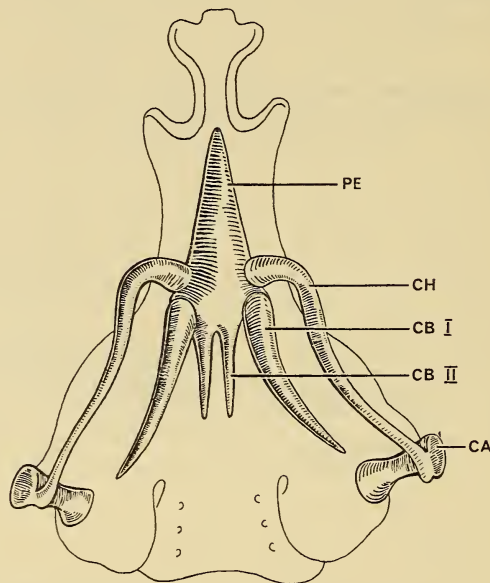


FIG. 3. *Sphenodon punctatus*, ventral view of hyobranchial skeleton (after Schauinsland).

C.A., columella auris; CB I-II, ceratobranchial I-II; C.H., ceratohyal; P.E., processus lingualis.

The condition found in *L. murrayi* would seem to resemble most closely that found in *Sphenodon*. This similarity, together with the phylogenetic relationship which exists between the ceratohyal and the columella auris and stapes in recent reptiles and mammals, respectively, and the fact that the processus interhyalis is the most consistent process of the reptilian columella auris, are the bases on which the assumption is made that the stapedia processes found in *Lystrosaurus* represent ossified ceratohyals.

The question arises whether the stapedial attachment in *L. murrayi*, *L. natalensis* and *L. verticalis*, represents the primitive condition or whether it represents a neotenic condition. The same question has been debated regarding the conditions found in the adult *Sphenodon* and the answers have been divergent; Schauinsland (1900), Wyeth (1924) and Goodrich (1930) declaring that it represented the primitive condition, while De Beer (1937) maintained that the condition must be 'associated with the degeneration of the tympanic membrane and therefore constitutes a secondary condition brought about by the arrest of development' (p. 241).

In many features of the skull *Sphenodon* shows that it is a relict of the past. It may be argued, therefore, that it retained also the primitive connexion between the ceratohyal and the sound-conducting apparatus and that this assumption is now borne out by the evidence uncovered in the fossil *Lystrosaurus* forms. However, the latter are highly specialized forms and as the condition found here is, to date, unique among anomodonts and is representative of some species of *Lystrosaurus* only, it may well represent a neotonic condition. Unfortunately we lack further information.

The further question arises as to whether *Sphenodon* uses the avenue provided by the hyoid-columella connexion for the transmission of sound to the internal ear, as it is known that full tympanic expansion of the cavum tympani does not occur during the ontogeny of *Sphenodon* and that a thick layer of tissue is left between the cavum tympani and the skin (Simonetta, 1963).

Although tests have frequently been conducted on the sensitivity of the ear in various reptiles no one has as yet attempted to find out whether the ceratohyal in *Sphenodon* acts as a sound-transmitting agent. This knowledge would be invaluable for any theory regarding sound perception and the presence or absence of the tympanum in *Lystrosaurus* for we cannot exclude the possibility that the persistence in *Sphenodon* of the embryonic connexion, whether it be the cause or effect of the non-development of the tympanum, may also be an indication of the existence of similar conditions in the fossil form.

Regarding his observations on *Sphenodon* Newman (1877) writes: 'When the tuatara inspires it greatly depresses the hyoid and trachea, thereby enlarging the pharyngeal cavity. By this means the tuatara inhales a large quantity of air, filling the lungs, mouth, trachea and the large pharyngeal cavity. This particular mode of respiring by depressing the hyoid bone (which with its cornua is very large) enables the tuatara to inhale sufficient air to remain under water for hours without coming to the surface to breathe' (p. 225).

It is not impossible, therefore, that the air contained in the expanded trachea could act as resonator for sound travelling through the water and as the hyoid apparatus is tense, such movement could be transmitted on to it and to the columella. When on land, where it frequents burrows, the lack of a tympanum would seem to indicate that sound waves are picked up directly from the substrate. Thus sound could be transmitted directly not only via the lower jaw and quadrate to the stapes but also via the hyoid apparatus.

Bone conduction is not uncommon in living burrowing and non-burrowing reptiles which lack a tympanum or have a reduced tympanic membrane. This has led to various changes in the composition of the middle ear structures in order to facilitate sound perception. In the non-burrowing lizards *Tympanocryptis*, *Aphaniotes*, *Cophotis*, *Lyriocephalus* and *Ceratophora* (Smith, 1938), loss of the tympanum is accompanied by reduction of the extracolumella to a vestige projecting from the stapes, but compensation is made through the attachment of the columella by the ossified dorsal and internal processes to the quadrate. In burrowing lizards, where loss of the tympanum is mostly accompanied by a reduction of the middle ear and Eustachian tube, the columella can be attached direct to the quadrate by means of the cartilaginous extra-columella (*Anniella*, Toerien, 1950) or by a ligament to the quadrate, supratemporal and otic capsule (*Scelotes*, Toerien, 1963) or by a ligament to the retroarticular process of the lower jaw (*Typhlosaurus*, Toerien, 1963). In others the columella itself is expanded and continued anteriorly to end either in the upper lip (*Typhlosaurus*, Toerien, 1963) or in the skin over the lower jaw (*Monopeltis*, Kritzing, 1945, *Rhineura*, Toerien 1963).

It is important to note too that none of the burrowing forms investigated by Toerien showed a reduction of the papilla basilaris (the actual organ of hearing in the inner ear) or of the stapes. The stapes, on the contrary, is often greatly increased in size. Although there are exceptions (the Australian burrowing lizard *Aprasia pulchella*, in which the middle ear is almost completely absent, has according to Underwood, 1957, only a tiny nodule which is presumably a vestige of the footplate of the stapes) it is nevertheless a significant observation. The tympanum is not essential for sound perception via the columella auris and Toerien's observation adds the possibility that the absence of the tympanum, whether caused by or contributing to, the reduction of the extra-columella does not affect the stapes and could even have a compensating effect on the development of the footplate. This is worth noting for the stapes seems unaccountably large in some anomodonts.

The connexion of the hyobranchial skeleton to the stapes in *Lystrosaurus* would seem to point to a system of sound transmission not based on sound perception via the tympanum. Sound waves were probably picked up by placing the head against the ground and transmission effected by bone conduction either via the lower jaw, the hyobranchial skeleton, or both.

There is reason to believe that a variable association between the stapes and ceratohyal could also have existed in some of the other anomodont genera but at this stage it would seem that a definite association was far more common in the genus *Lystrosaurus*.

SUMMARY

A description is given of a rod-like process on the stapes of *Lystrosaurus*, an extinct mammal-like reptile from the Beaufort Beds of the Karoo of South Africa. It is suggested that the bone represents the ossified ceratohyal. This

stapedial process is regarded as highly significant and it is claimed that it throws new light on the method of sound transmission in this genus of Anomodont Therapsids.

ACKNOWLEDGEMENTS

This project and the publication of these results were in part financed by a grant received from the South African Council for Scientific and Industrial Research. For this I wish to thank the Council. I also wish to thank Dr. M. E. Malan of the Department of Zoology, University of Stellenbosch for criticism of the manuscript and for helpful suggestions and Mrs. I. Rudner and Mr. C. Gow of the South African Museum for preparation of the fossils used in this investigation.

REFERENCES

- BARRY, T. H. 1963. On the variable occurrence of the tympanum in recent and fossil tetrapods. *S. Afr. J. Sci.* **59**: 160-175.
- BENDER, O. 1911. Über Herkunft und Entwicklung der Columella auris bei *Testudo gracilis*. *Anat. Anz.* **40**: 161-177.
- COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 321.
- DE BEER, G. R. 1937. *The development of the vertebrate skull*. Oxford University Press, London.
- EWER, R. F. 1961. The anatomy of the Anomodont *Daptocephalus leoniceps* (Owen). *Proc. zool. Soc. Lond.* **136**: 375.
- GOODRICH, E. S. 1930. *Studies on the structure and development of vertebrates*. Constable & Co., London.
- KRITZINGER, C. C. 1945. The cranial anatomy and kinesis of the South African amphisbaenid *Monopeltis capensis* Smith. *S. Afr. J. Sci.* **42**: 175.
- NEWMANN, A. K. 1877. Notes on the physiology and anatomy of the Tuatara (*Sphenodon guntheri*). *Trans. N. Zealand Int.* **10**: 222-239.
- SCHAUINSLAND, H. 1900. Beiträge zur Entwicklungsgeschichte der Hatteria. *Arch. Mikr. Anat. u. Entw.* vol. **57**.
- SIMONETTA, A. 1963. Cranial kinesis and morphology of the middle ear: two possibly related features. *Evolution* **17**: 580-587.
- SMITH, L. W. 1914. The origin and development of the columella auris in *Chrysemys marginata*. *Anat. Anz.* **46**: 457-560.
- SMITH, M. A. 1938. Evolutionary changes in the middle ear of certain agamid and iquanid lizards. *Proc. zool. Soc. Lond.* **108**: 543.
- TOERIEN, M. J. 1950. The cranial morphology of the Californian lizard—*Anniella pulchra* Gray. *S. Afr. J. Sci.* **46**: 321.
- TOERIEN, M. J. 1963. The sound-conducting systems of lizards without tympanic membranes. *Evolution* **17**: 540-547.
- UNDERWOOD, G. 1957. On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the squamata. *Morph.* **100**: 207.
- WYETH, F. J. 1924. The development of the auditory apparatus in *Sphenodon punctatus*; with an account of the visceral pouches, aortic arches, and other accessory structures. *Phil. Trans. roy. Soc. Lond.* **212**: 259-368.